Loss of Eelgrass in Casco Bay, Maine, Linked to Green Crab Disturbance

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Abstract - Over half of the *Zostera marina* (Eelgrass) cover disappeared from Casco Bay, ME, largely between 2012 and 2013. Eelgrass decline coincided with a population explosion of the invasive crab *Carcinus maenas* (European Green Crab). Green Crabs have been found to damage Eelgrass in Atlantic Canada through foraging activity, but destruction of established beds had not been documented in Maine. My objective was to determine whether loss of Eelgrass from Casco Bay was related to Green Crab disturbance. In September 2013, I transplanted Eelgrass shoots inside and outside of replicate Green Crab exclosures in a formerly vegetated area of upper Casco Bay. Following 26 d, mean survival of Eelgrass inside the exclosures was 82% and outside the exclosures was 24%. The mean plastochrone interval (time between formation of 2 successive leaves) of undamaged shoots was the same inside and outside the exclosures, and was comparable to published values from healthy Eelgrass beds in New England. Results implicate Green Crab bioturbation as a leading cause of Eelgrass loss from this system.

Introduction

Zostera marina L. (Eelgrass) forms extensive meadows in coastal and estuarine waters throughout New England and Atlantic Canada (Short and Short 2003). Ranked among the most productive plant communities on the planet, Eelgrass is valued as critical habitat for many ecologically and economically important fish and shellfish species (Moore and Short 2006, Orth et al. 2006a). Waterfowl, wading birds, and shore birds also depend on the rich food resources found in Eelgrass beds (Erwin 1996, Seymour et al. 2002). Like other seagrass species, Eelgrass also absorbs nutrients, baffles waves and currents, stabilizes bottom sediments, and serves as a natural and highly efficient carbon sink while buffering the local pH environment (Hendriks et al. 2014, Mcleod et al. 2011, Orth et al. 2006a). Because of these diverse ecological functions, loss of Eelgrass can have wide-ranging consequences, including reduced fish and wildlife populations, degraded water quality, increased shoreline erosion, and reduced capacity to remove anthropogenic carbon dioxide emissions and mitigate impacts of ocean acidification (Duarte 2002, Duarte et al. 2013, Greiner et al. 2013, Orth and Moore 1983).

Eelgrass occurs in the low intertidal and shallow subtidal zones along much of Maine's shoreline (MDMR 2012). Historically, Eelgrass reached one of its greatest statewide extents in Casco Bay, located in southern Maine (Fig. 1). Mapping based on aerial photography acquired in 2001 and 2002 showed 3338 ha of Eelgrass in Casco Bay (CBEP 2005). Much of the Eelgrass occurred in the broad

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intertidal and subtidal flats of the upper bay; the intertidal meadows represented some of the largest expanses of intertidal Eelgrass in the western North Atlantic (Short and Short 2003). In July of 2013, a dramatic loss of Eelgrass was discovered. Remapping from aerial photography acquired in August 2013 revealed only

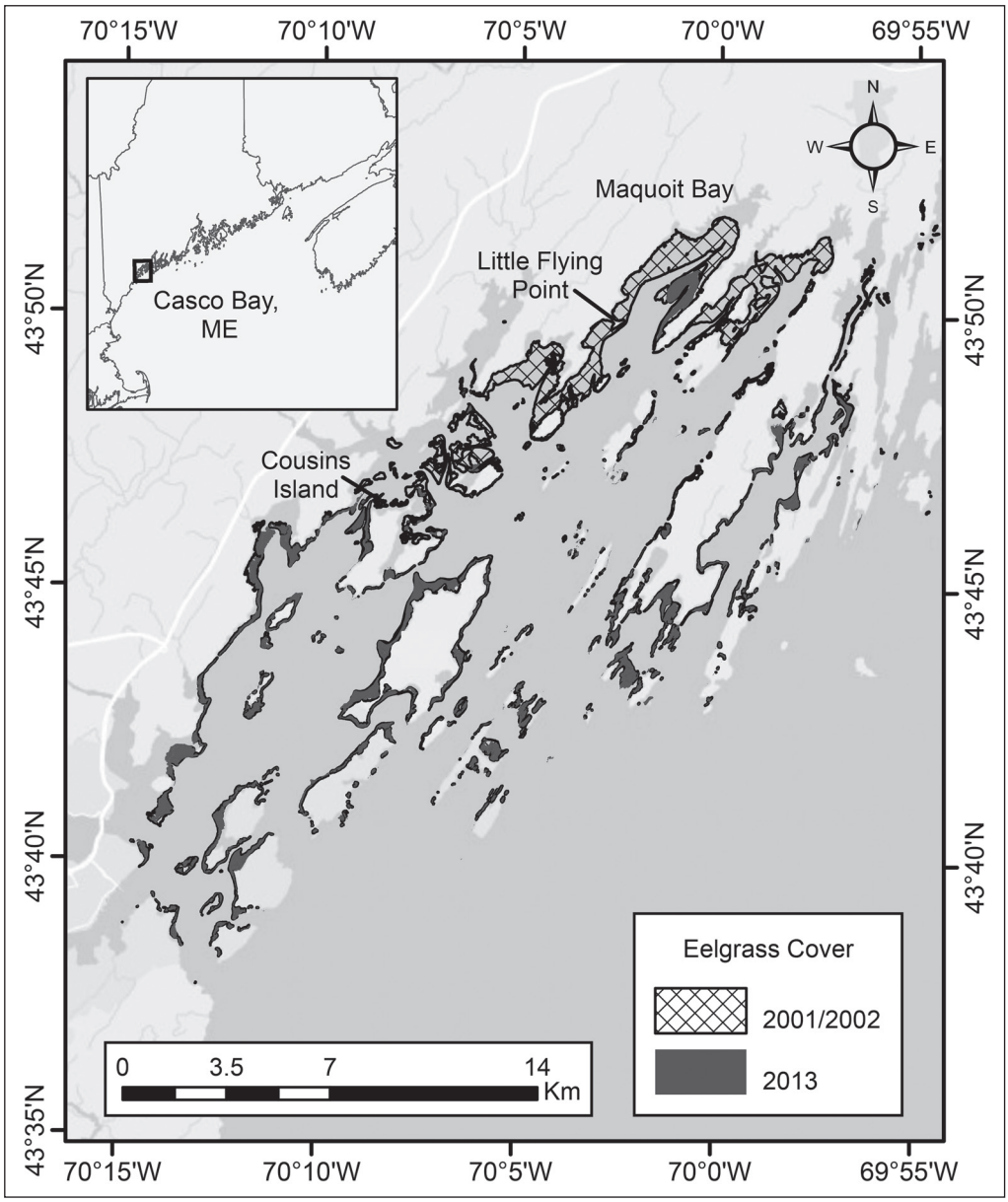

Figure 1. Study area in Casco Bay, ME, showing distribution of Eelgrass based on aerial photography acquired in 2001 and 2002 (crosshatched; MDMR 2012) and in August 2013 (shaded; Barker 2013, MDEP 2013). Where 2013 coverage is mapped, it overlays and largely coincides with the 2001/2002 distribution. The Eelgrass persisting in Maquoit Bay in 2013 was mapped at <10% cover (MDEP 2013). The arrow at Cousins Island points to the Eelgrass collection site.

1477 ha of Eelgrass in all of Casco Bay (Barker 2013, MDEP 2013), with nearly complete loss of Eelgrass from the bay's uppermost reaches (Fig. 1). Reconstruction of local observations indicated a rapid Eelgrass decline that occurred largely between 2012 and early 2013.

The near-complete disappearance of Eelgrass from upper Casco Bay coincided with a population explosion of the invasive crab, *Carcinus maenas* (L.) (European Green Crab, hereafter, Green Crab), in Casco Bay and other areas of the Maine coast (MDMR 2013, Webber 2013). The Green Crab was introduced to New York and southern New England in the early 1800s, and by the early 1900s had expanded its range northward to Casco Bay (Scattergood 1952). Dramatic increases in Gulf of Maine Green Crab populations in the 1930s, 1950s, and 1970s occurred during periods of sea-surface temperature warming, with subsequent population declines following unusually cold winters (Berrill 1982, Welch 1968). In the early 1950s, precipitous declines in populations of *Mya arenaria* L. (Soft-shell Clam) in New England were correlated with the increased abundance of Green Crabs (Glude 1955, Ropes 1968, Welch 1968). The most recent Green Crab population boom in Maine was similarly associated with warmer sea-surface temperatures (Beal 2014, MDMR 2013). Although no Green Crab monitoring was in place in Casco Bay in 2012 and early 2013, shellfish harvesters and Maine shellfish managers reported extremely high Green Crab densities in near-shore coastal habitat (Beal 2014; J.K. Kanwit, ME Department of Marine Resources and Chair of the Governor's Task Force on the Invasive European Green Crab, Augusta, ME). In 2013, Soft-shell Clam surveys in various locations in upper Casco Bay documented depleted Soft-shell Clam stocks and virtual absence of small individuals of young age-classes (Beal 2014, Devereaux 2013, MER Assessment Corporation 2013), a pattern that was also observed in the 1950s resulting from intensive Green Crab predation (Glude 1955). In an area of ~50 ha in upper Casco Bay (in the Harraseeket River, South Freeport, ME), a 2013 trapping study conducted from late May to early November yielded a total of 5939 kg of Green Crabs from 300 hauls, with an average catch per trap of 4.7 kg (Beal 2014). A 24-h, statewide Green Crab trapping survey that was coordinated by the Maine Department of Marine Resources on 1 August 2013 yielded catch rates per trap of up to 181 Green Crabs from Casco Bay locations (Webber 2013).

Green Crabs are known to damage and uproot Eelgrass shoots while digging in the sediment for benthic prey (Davis et al. 1998, Malyshev and Quijón 2011), and juveniles may also cut off shoots while grazing directly on Eelgrass meristems (Malyshev and Quijón 2011). Such foraging activity by high densities of Green Crabs has been shown to cause drastic declines of Eelgrass from some bays in Nova Scotia, Canada (Garbary et al. 2014, MTRI and Parks Canada 2014). At the time of Eelgrass disappearance from Casco Bay, destruction of established beds by Green Crabs had not been documented in Maine. However, I recovered Eelgrass shoots from the shoreline of upper Casco Bay with clipped and frayed bases characteristic of Green Crab damage (Fig. 2; cf., Davis et al. 1998, Garbary et al. 2014), suggesting Green Crabs as a local source of disturbance. Thus, the goal of this study was

to determine whether Green Crab bioturbation may have caused the loss of Eelgrass in upper Casco Bay.

The lack of data on Green Crab densities in upper Casco Bay during the Eelgrass decline hindered direct tests of the potential effects of Green Crab activity on Eelgrass disappearance. Therefore, in September 2013, I conducted a field experiment to test whether environmental conditions in upper Casco Bay would support Eelgrass growth in the absence of Green Crab disturbance. I transplanted Eelgrass shoots from a persistent bed in mid-Casco Bay to locations inside and outside of protective crab-exclosures in a formerly vegetated site in the upper bay, and

Figure 2. Eelgrass shoots collected from the shoreline of upper Casco Bay on 30 July 2013 and 12 August 2013 with clipped (top photos) and frayed (bottom photos) bases characteristic of Green Crab damage.

harvested the plants after a 26-d growth interval. A comparison of Eelgrass growth and survival between protected and unprotected treatments provided indirect evidence for the role of Green Crabs in decline of Eelgrass habitat in upper Casco Bay.

Field-Site Description

This experiment was conducted in Maquoit Bay, which is the uppermost embayment of western Casco Bay (Fig. 1). Maquoit Bay is a shallow estuary encompassing 1013 ha with broad intertidal and subtidal flats and a narrow central channel. The tidal range is approximately 4 m, and bottom sediments are predominantly mud (clay and silt; Kelley et al. 1987, Larsen et al. 1983, Neckles et al. 2005). Historically, Eelgrass extended continuously from the low intertidal zone to depths of about 3 m below mean low water (MLW). In 2001, there were 570 ha of Eelgrass mapped in Maquoit Bay (Neckles et al. 2005), and aerial photographs acquired in November 2009 showed little change in Eelgrass distribution up to that time (CBEP 2010). Most of the Eelgrass in Maquoit Bay was mapped at 70–100% cover in 2001 (MDMR 2012). Although there were no formal assessments of Eelgrass coverage between 2009 and the discovery of denuded sediments throughout upper Casco Bay in July 2013, local observations by shoreline residents, shellfish harvesters, town officials, and a college biology class pinpointed the most substantial Eelgrass loss in Maquoit Bay as occurring from summer 2012 into early 2013. Mapping from aerial photographs acquired in August 2013 revealed that only 96 ha of Eelgrass remained (Fig. 1), all of which occurred at less than 10% cover (MDEP 2013).

I installed experimental exclosures in the cove north of Little Flying Point in southwestern Maquoit Bay (Fig. 1). In 2009, the Eelgrass bed had covered the entire cove (CBEP 2010), but in July 2013 the cove was completely devoid of vegetation. I placed the exclosures in the shallow subtidal zone at a depth of about 0.3 m below MLW. The seawater salinity was 30 ppt and the bottom sediments were uniformly mud.

Methods

Experimental design

I planted Eelgrass shoots in plots that were either protected (inside exclosures) or unprotected (outside exclosures) from potential Green Crab disturbance. I established 3 replicates of each type of plot along a 33.2-m transect that was 340 m from shore and parallel to the shoreline, so that all plots were at similar depths (Fig. 3A). The protected plots were inside square crab-exclosures that were 12 m apart along the transect, and the unprotected plots were located 2 m outside of the exclosures along the same transect. I marked each unprotected plot with a single wooden stake.

The exclosures were framed with lumber (2 x 4s); the side panels were 0.46 m tall, 2.4 m wide, and constructed with corner posts that extended 0.46 m below the bottom of the frame. The side walls were rigid plastic mesh with 0.5-cm openings. I anchored the exclosures in place by driving the corner posts into the mud so that the bottom of exclosure frame lay in the sediment. To prevent Green Crabs from

climbing into the exclosures, I attached a 15-cm strip of aluminum flashing to the top of each wall and bent it outwards at an angle, essentially forming a downward-opening pocket around the exclosure rim. To prevent Green Crabs from burrowing into the exclosures, I staked a 25-cm-wide strip of plastic mesh flat onto the sediment surface along the outside border of each wall.

I installed the exclosures in the field on 23 August 2013, and allowed them to stabilize for 12 d before I transplanted the Eelgrass shoots into the experimental plots. The growth experiment extended from 5 September 2013 to 1 October 2013 (26 d). I monitored Green Crabs at the study site as catch per unit effort using crab traps deployed continuously from 23 August to the end of the experiment. I set a crab trap inside each exclosure (Fig. 3B) and set 2 traps outside the exclosure array (Fig. 3A). The traps were rectangular (71 cm x 30 cm x 30 cm) with a single opening (8 cm x 13 cm). They were constructed of plastic-coated steel wire and heavy enough to stay in place on the substrate without weights. At the beginning of the pre-experimental stabilization period, I baited the traps with equal amounts of Soft-shell Clams and groundfish-processing waste—bodies with filets removed, heads, and skins of *Melanogrammus aeglefinus* (L.) (Haddock), *Gadus morhua* L. (Atlantic Cod), and *Pollachius virens* (L.) (Pollack). Green Crab monitoring during this period served to determine the effectiveness of the exclosures in preventing crab entry. To minimize attracting Green Crabs into the exclosures during the growth experiment, I discarded all bait remaining in all the traps when the Eelgrass was transplanted into the experimental plots. In addition to documenting the abundance of Green Crabs as a potential disturbance to Eelgrass, trapping during the growth experiment was an effort to confine Green Crabs that entered the exclosures away from the Eelgrass plants. I removed and counted all Green Crabs from the traps twice per week, and cleaned any accumulated sediment off the mesh walls of the exclosures with a scrub brush.

Eelgrass transplanting

I collected Eelgrass shoots on 4 September 2013 from a persistent bed off Cousins Island in mid-Casco Bay, which was the closest extensive, dense Eelgrass bed to the study site (Fig. 1). I collected shoots from the shallow subtidal zone at a depth comparable to that at the exclosure location. I gently uprooted ~120 shoots by hand with 3–5 cm of rhizome intact (Davis and Short 1997). Maintaining Eelgrass at low salinities minimizes potential infection and spread of wasting disease (caused by the naturally-occurring slime mold *Labyrinthula zosterae* Porter and Muehlstein) in the collected shoots (Burdick et al. 1993); therefore, I diluted seawater from the collection site with distilled water to 12 ppt as a storage medium. I transported and stored the plants overnight in a large tub of aerated, diluted seawater at 20 °C.

I prepared Eelgrass planting units and transplanted them into the experimental field sites on 5 September 2013, using a modification of the horizontal-rhizome transplant method (Davis and Short 1997). During preparation of the planting units, I gradually added seawater from the collection site to the Eelgrass storage medium to increase the salinity to the ambient field strength; the salinity was adjusted from 12

ppt to 30 ppt over 6 h. A planting unit consisted of 5 pairs of shoots attached to a 50-cm length of 0.95-cm diameter steel reinforcing bar; thus, each planting unit had 10 shoots. I attached shoot pairs to the bar with plastic cable ties at 10-cm intervals with the rhizomes aligned parallel to the bar and pointing in opposite directions. Eelgrass

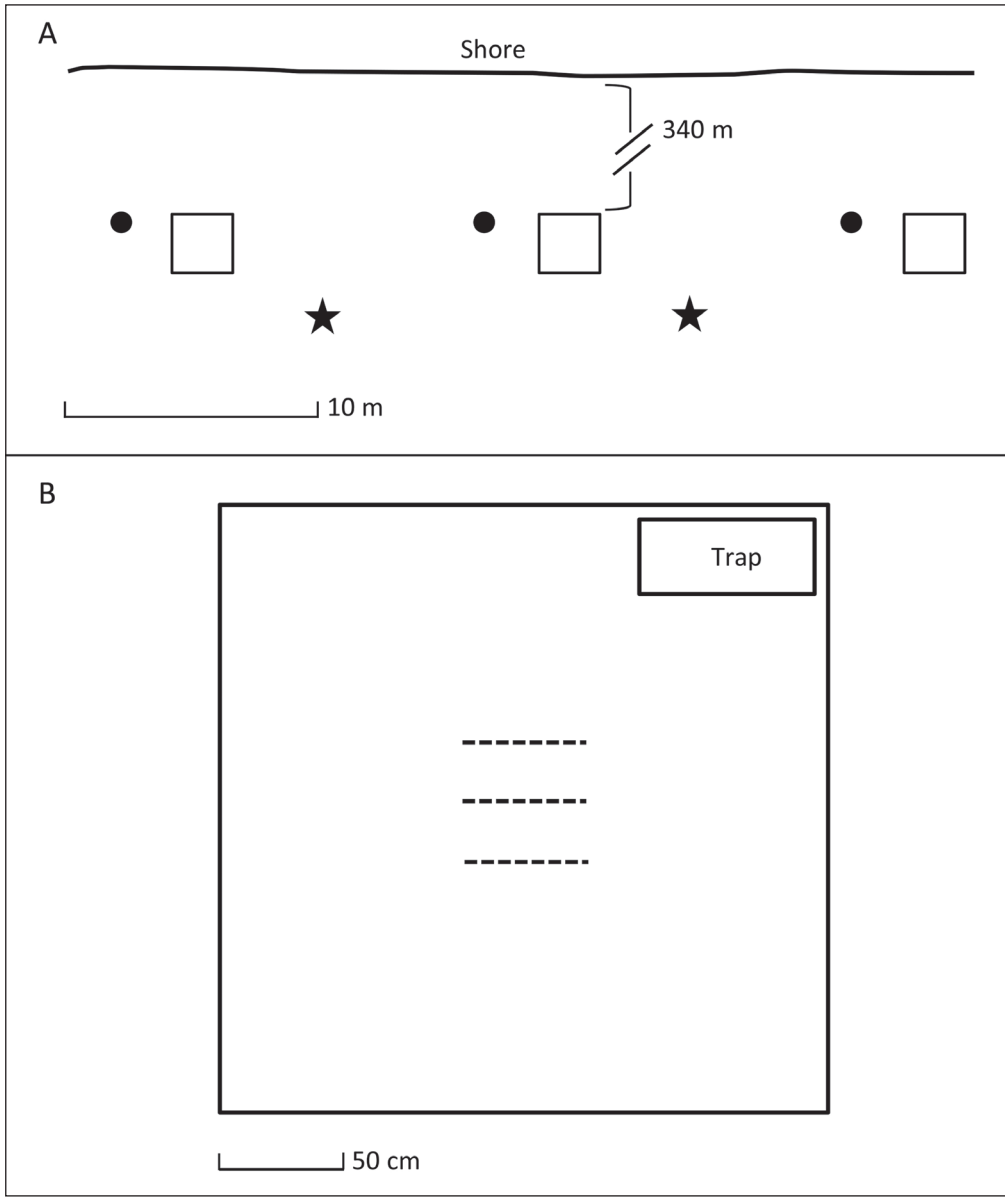

Figure 3. Design of the field experiment. (A) Position of exclosures (squares) and unprotected sites (black circles) along a transect 340 m from shore. Stars represent locations of Green Crab traps set outside of the exclosures. Size of circles and stars is not to scale. (B) Detail of a single exclosure showing the position of planting units (dashed lines) and Green Crab trap. The trap opening is on the short side of the trap facing towards the inside of the exclosure.

grows by successive formation of leaves at identifiable nodes along the rhizome and lengthening of the rhizome sections between the nodes, termed the internodes (Duarte et al. 1994). I fastened shoots to the bar at a point immediately distal to the second complete rhizome node; thus, each shoot had 1 complete rhizome segment (node plus internode) between the basal leaf/rhizome meristem and the cable tie. In this way, the cable ties served effectively as rhizome tags for identifying new rhizome tissue produced during the experiment (Short and Duarte 2001).

I transplanted the Eelgrass planting units at the study site 24 h after initial shoot collection. Three planting units were assigned haphazardly to each experimental plot; thus, the experimental design consisted of 3 replicate plots of each treatment (protected and unprotected), with 3 subsamples (Eelgrass planting units) per plot. I installed the planting units by pressing the bars and attached rhizomes into the top 2 cm of the sediment and anchoring the ends of the bars to the substrate with U-shaped wire staples. I installed the planting units parallel to one another and 25 cm apart, so that the 3 planting units occupied a 50 cm x 50 cm square (Fig. 3B). The planting units inside the exclosures were 0.95 m away from the walls in all directions.

Eelgrass measurements

I observed the condition of the Eelgrass planting units after 10 d and 19 d of growth by snorkeling over the planting units at low tide. At the end of the experiment I harvested all planting units for quantitative analysis. I measured survival of individual planting units as the proportion of the original 5 pairs of Eelgrass shoots with at least 1 shoot remaining. I assessed planting-unit survival using an analysis of variance for subsampling model, with treatment effects determined using the experimental error, and employed residual analysis to confirm that the basic assumptions of analysis of variance were met (Kutner et al. 2004).

I used only undamaged Eelgrass shoots to test whether environmental conditions in upper Casco Bay would support Eelgrass growth in the absence of Green Crab disturbance. I assessed all surviving shoots for the presence of clipped leaves or shredding along the leaf axis, which would characterize Green Crab damage (Fig. 2). For all undamaged shoots, I recorded the total number of complete rhizome segments present between the meristem and the cable tie. To decide whether all undamaged shoots could be pooled for reporting purposes, I used a *t*-test to determine whether there was a difference in the number of rhizome segments in front of the cable tie between shoots growing inside and outside the exclosures. For each undamaged shoot, I calculated the minimum and maximum number of new rhizome segments that could have been produced during the experimental growth interval; the range in the potential number of new segments on a given shoot accommodated an unknown amount of rhizome tissue present between the first rhizome node and the shoot meristem on planting (Day 0), which varied among shoots from almost indiscernible to almost the length of a full internode. The potential maximum number of new rhizome segments produced during the experiment equaled the total number of segments in front of the cable tie (i.e., between the cable tie and the meristem) at harvest (Day 26) minus

1, which accounted for the single complete rhizome segment in front of the cable tie at Day 0 and no rhizome tissue present initially between the first node and the meristem. The potential minimum number of new segments produced equaled the total number of rhizome segments in front of the cable tie on Day 26 minus 2, which accounted for both the complete segment in front of the cable tie and a nearly complete segment between the first node and the meristem on Day 0. In Eelgrass, a new leaf is produced with each new rhizome segment (Duarte et al. 1994, Short and Duarte 2001); thus, I derived the plastochrone interval, or the time interval (d) between the formation of 2 successive leaves on the shoot, as the growth interval (26 d) divided by the number of new rhizome segments.

Environmental factors

I measured diffuse downwelling attenuation of photosynthetically available radiation (PAR) at the study site twice during the growth experiment (15 and 28 September). I took measurements at the midpoint of the exclosure transect when the water was about 1.25-m deep (on a falling tide on 15 September and a rising tide on 28 September). I measured duplicate or triplicate profiles of downwelling photosynthetic photon-flux density using a LI-192SA underwater quantum sensor (LI-COR, Lincoln, NE) within 1.5 h of solar noon (Carruthers et al. 2001). I made measurements every 20 cm from 10 cm below the water surface to about 25 cm above the ocean bottom; measurements at each depth were integrated over 15 sec. Simultaneous measurements of incident PAR were made using a LI-190SA terrestrial quantum sensor (LI-COR) to account for any changes in incident solar irradiance over the period of time needed to complete a full water-column profile. I calculated the attenuation coefficient of downwelling PAR (K_d) as the slope of the least squares regression relating ln (I_z/I_{air}) to depth in meters, where I_z is the irradiance at depth z and I_{air} is the incident irradiance in air.

At the end of the experiment I collected sediment samples from the center of each experimental replicate. I collected samples from the top 10 cm of sediment using a 2.5-cm-diameter syringe corer (i.e., a 60-cc syringe with the graduated tip cut off flush with the zero volume mark); samples were frozen and stored for 2 months. Prior to analysis, I thawed the samples under refrigeration and homogenized them. I determined organic content by loss on ignition following combustion for 4 h at 450 °C (Erftemeijer and Koch 2001), and employed a *t*-test to compare the mean organic content of the sediments in the protected and unprotected plots.

I continuously measured water temperature at the study site throughout the experiment using an Onset TidbiT®v2 temperature logger (Onset Corporation, Bourne, MA) attached to a stake installed at the end of the exclosure transect; temperature was recorded at 30-min intervals. The logger was near the bottom of the water column so that it remained submerged during the study period. Eelgrass die-offs in some areas have been associated with sustained high water temperatures (Moore et al. 2014, Nejrup and Pedersen 2008, Reusch et al. 2005); thus, I derived the maximum daily water temperatures in Casco Bay during July and August, 2002–2012 from continuous data recorded at the National Oceanic and Atmospheric

Administration tide station in Portland, ME (NOAA CO-OPS 2013). The station is located at the southern end of Casco Bay (43°39'24"N, 70°14'48"W), at the end of the Maine State Pier. Temperature was recorded at 6-min intervals at a depth 3.4 m below mean lower low water. I created cumulative percentage distributions of daily high water temperatures during July and August from frequencies within 1-degree bins. In addition, I interviewed citizens residing along the shoreline of upper Casco Bay regarding observations of potential physical disturbance to Eelgrass during 2012 and early 2013.

Results

Effectiveness of exclosures

I captured an order of magnitude more Green Crabs in baited traps that were deployed outside the exclosures than inside the exclosures during the pre-experimental period (Table 1). Thus the exclosures limited, but didn't completely prevent, Green Crab access. Continuous monitoring with unbaited traps during the experimental period showed that Green Crabs persisted in the study area throughout the growth experiment, and that even the Eelgrass planting units protected by the exclosures were potentially subjected to some level of Green Crab disturbance (Table 1). There was no discernible evidence of exclosure influence on water flow in the protected sites; during biweekly site-visits I observed the shoots inside and outside the exclosures to be bent at similar angles, and there were no visible differences between treatments in the level of sediment accumulated on the leaves.

Eelgrass survival and growth

Preliminary observations revealed early differences in Eelgrass survival inside and outside the exclosures. After 10 d of growth, each of the protected planting units still had 5 pairs of shoots, whereas most of the unprotected planting units had ≤2 pairs of shoots. Some shoot bases with the leaves clipped off were evident

Table 1. Responses by Green Crabs and Eelgrass inside and outside of experimental exclosures. #/baited trap = total number of Green Crabs caught per baited trap during pre-experimental period (n = 3 inside, n = 2 outside); #/unbaited trap = total number of Green Crabs caught per unbaited trap during experimental period (n = 3 inside, n = 2 outside); # undamaged shoots = total number of surviving shoots that were undamaged (out of initial 90 shoots per treatment); # damaged shoots = total number of surviving shoots that showed evidence of Green Crab damage (out of initial 90 shoots per treatment). Values for Green Crabs are mean (range) of total number caught per trap in individual traps deployed continuously during the pre-experimental period (23 August–5 September) and the experimental period (5 September–1 October); values for planting-unit survival are mean ± SE; values for undamaged and damaged shoots are total counts across all replicates.

	Protected plots inside exclosures	Unprotected plots outside exclosures
#/baited trap	27 (22–32)	242 (213–272)
#/unbaited trap	17 (9–30)	34 (31–37)
Planting-unit survival (%) (n = 3 plots per treatment)	82 ± 14	24 ± 14
# undamaged shoots	47	10
# damaged shoots	10	5

among the unprotected planting units. By 19 d of growth, nearly all of the protected planting units still had ≥4 shoot pairs, whereas some of the unprotected planting units were devoid of vegetation. At the end of the experiment, survival of the planting units in the protected plots in the exclosures was more than 3 times that of the planting units that were unprotected from Green Crabs outside the exclosures (Table 1; $F = 7.86$, $P = 0.049$), and most of the surviving shoots that showed no sign of Green Crab damage were inside the exclosures (Table 1). Where shoots were missing from the planting units, rhizomes with clipped-off shoots or shoot bases with clipped-off leaves were often still attached.

There was no difference in the mean number of rhizome segments in front of the cable tie between undamaged shoots from within (4.2 ± 0.1 SE) and outside (3.8 ± 0.2 SE) the exclosures ($t = 1.62$, $P = 0.111$), thus I pooled all 57 undamaged shoots (Table 1) for subsequent analysis. The undamaged shoots produced a mean maximum of 3.1 (± 0.1 SE) and a minimum of 2.2 (± 0.1 SE) new rhizome segments during the 26-d growth interval, which corresponded to a mean plastochrone interval of 8.8 d (± 0.3 SE) to 14.1 d (± 0.9 SE) (Table 2).

Environmental factors

The attenuation of downwelling PAR measured during the growth experiment varied from 0.63 m^{-1} (mean of 2 profiles on 15 September) to 0.73 m^{-1} (mean of 3 profiles on 28 September), resulting in 23–19% of solar PAR insolation available at the transplant depth at mid-tide (i.e., a depth of 2.3 m). The average daily seawater temperature dropped from 18.4 °C to 15.4 °C from 6–17 September, and then remained at about 15 °C through harvest on 1 October. The maximum seawater temperature recorded during the growth experiment was 20.8 °C and the minimum was 13.2 °C. The sediment organic content was 4.9% (± 0.04 SE) inside the exclosures and 4.6% (± 0.35 SE) at the unprotected sites outside the exclosures, with no significant difference between experimental treatments ($t = 0.71$, $P = 0.550$).

The median daily high water temperature recorded during July and August at the Portland, ME, monitoring station ranged from 15.3 °C in 2004 to 19.0 °C in 2012 (Table 3). There was considerable overlap of the cumulative percentage distributions of summertime daily high temperatures from 2003 through 2009, so alternate years are presented within this range for clarity (Fig. 4). During 2011 and

Table 2. Mean Eelgrass plastochrone interval (time interval between the formation of 2 successive leaves on a shoot) measured at locations in New England during September.

Location	Growth period(s)	Plastochrone interval (days)	Reference
Maquoit Bay, Freeport, ME	Single growth period (26 d) in September 2013	8.8–14.1	This study
Fishing Island, Kittery, ME	Two growth periods (18 d, 19 d) in September 2000	12.6–15.5	Gaeckle and Short (2002)
Waquoit Bay, MA	Single growth period (27–36 d) in September 1998, in each of 4 estuaries	10.1–15.3	Hauxwell et al. (2006)

2012, a greater percentage of days reached higher temperatures than during earlier years. The maximum temperatures were recorded in 2012, with the daily high temperature reaching between 20 °C and 21 °C on 5 days.

Discussion

Loss of Eelgrass from Casco Bay

Eelgrass survival in Maquoit Bay was enhanced substantially by protection from Green Crabs. As evidenced by the capture of some Green Crabs inside the

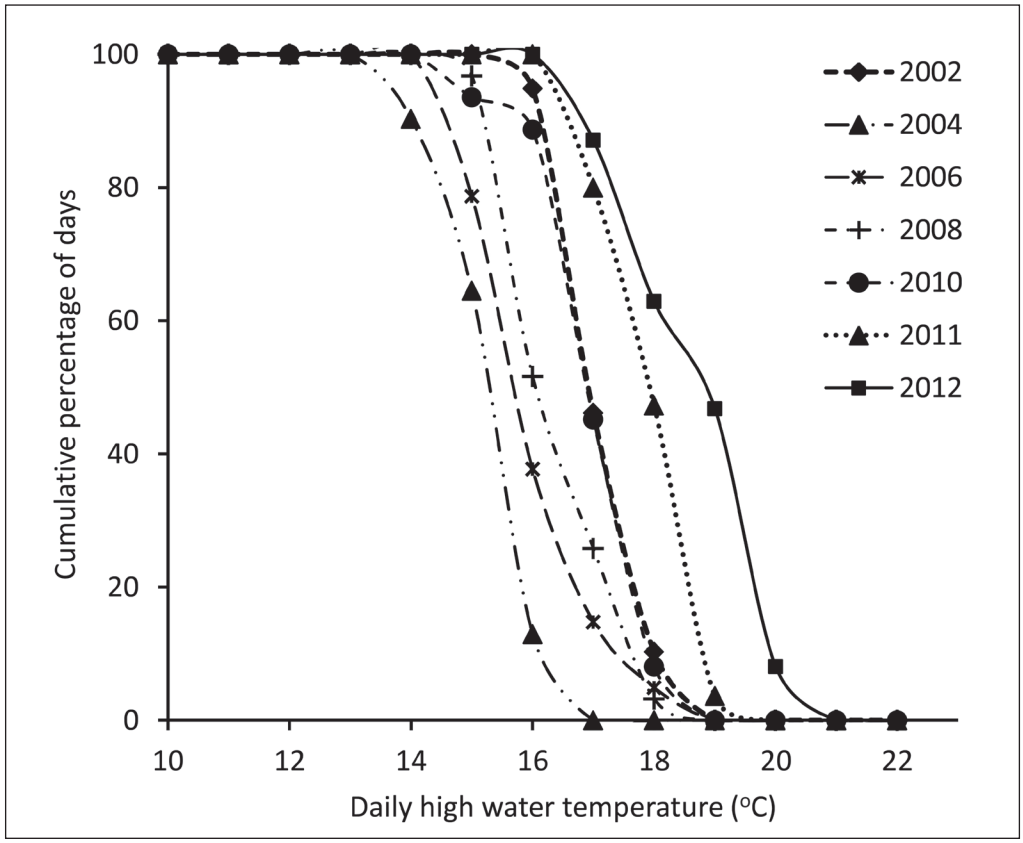

Figure 4. Cumulative percentage distributions of summertime (July–August) daily high temperatures of seawater measured at the NOAA tide station at the southern end of Casco Bay during selected years. Plots indicate the percentage of days in July and August with daily high temperatures above the values indicated along the *x*-axis.

Table 3. Median daily high temperature of seawater recorded during July and August at the NOAA tide station at the southern end of Casco Bay. Eelgrass was present throughout the bay from 2002 through at least 2010, and the major Eelgrass loss occurred from 2012 through early 2013.

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
Median daily high temp (°C)	17.0	15.6	15.3	15.8	15.7	15.7	16.2	15.9	16.9	18.0	19.0
n	39	62	62	62	61	61	62	62	62	55	62

exclosures during the experimental growth period (Table 1), the exclosure fencing did not isolate Eelgrass completely from potential disturbance; a proportion of the surviving shoots and many of the remnant bases of shoots that were lost from inside and outside the exclosures showed characteristic signs of Green Crab damage. Thus, it is likely that disappearance of the planting units within both treatments was caused by Green Crab disturbance. The plastochrone interval I measured on Eelgrass shoots that were not subject to Green Crab disturbance was comparable to published values from healthy Eelgrass beds in New England measured at the same time of year (Table 2). These results showed that in the absence of Green Crab disturbance, environmental conditions in Maquoit Bay following the extensive Eelgrass decline remained conducive to at least short-term growth and survival of Eelgrass.

Although Eelgrass is susceptible to various natural and anthropogenic disturbances (Orth et al. 2006a, Short and Wyllie-Echeverria 1996), multiple lines of evidence ruled out other acute environmental factors as causing Eelgrass loss in upper Casco Bay. For example, the most prevalent cause of seagrass loss worldwide is cultural eutrophication and consequent reduction in the amount of light available for seagrass photosynthesis (Burkholder et al. 2007, Waycott et al. 2009). An early sign of reduced light penetration to seagrass leaves is a decrease in the seagrass depth limit (Borum 1996, Dennison 1987, Sand-Jensen and Borum 1991). In Maquoit Bay, the depth limit of the Eelgrass meadow increased between 1993 and 2001 (Neckles et al. 2005) and then remained stable through 2009 (CBEP 2010), and in 2013 the only Eelgrass remaining was a small patch, albeit sparse, that extended to the deepest bed contour (Fig. 1); these temporal and spatial patterns are inconsistent with reduced light availability stemming from watershed inputs. Eutrophication can also lead to sediment organic enrichment and ultimate accumulation of phytotoxic sulfides with deleterious effects on Eelgrass (Holmer and Laursen 2002, Koch 2001, Mascaró et al. 2009), but the sediment organic content measured during this study within an area of Maquoit Bay that lost Eelgrass (4.6–4.9%) was unchanged from that measured at the same site in 2000, prior to the Eelgrass decline (4.8–5.4%; H. Neckles, unpublished site-means in the cove north of Little Flying Point that contributed to the bay-wide range of 4.0–5.8% reported in Neckles et al. 2005). There were no reports of any major direct physical disturbance to Eelgrass from either anthropogenic (e.g., trawling or dragging activity) or natural (e.g., storms or ice scour) activities during the period of vegetation loss (D. Devereaux, Brunswick Department of Marine Resources and Harbor Management, Brunswick, ME, pers. comm.). I also found no evidence of significant Eelgrass wasting disease (i.e., infection of younger inner leaves; Burdick et al. 1993) on any plants washed up on the shore of upper Casco Bay or in the persistent Eelgrass bed from which I collected experimental shoots.

High water-temperatures can adversely impact Eelgrass metabolism, causing reductions in photosynthetic performance (Evans et al. 1986, Nejrup and Pedersen 2008, Winters et al. 2011), ratio of photosynthesis to respiration (Marsh et al. 1986), meristematic oxygen content (Greve et al. 2003), and shoot density and

growth (Bergmann et al. 2010, Bintz et al. 2003, Ehlers et al. 2008, Nejrup and Pedersen 2008). Consequently, Eelgrass declines have been documented following even fairly short-term exposure to unusually high summer temperatures (Moore and Jarvis 2008, Moore et al. 2014, Reusch et al. 2005). The temperature thresholds associated with loss of Eelgrass cover vary with latitude: studies in northern Europe found reduced Eelgrass growth after 6 weeks at temperatures above 20 °C (Nejrup and Pedersen 2008) and a 44% reduction in shoot density after 4 weeks at 25 °C (Ehlers et al. 2008), and studies in southern Virginia reported Eelgrass die-offs following 1- to 2-week exposures to temperatures above 28 °C (Moore and Jarvis 2008, Moore et al. 2014). Although summertime water temperatures in Casco Bay reached higher daily maxima during the Eelgrass decline in 2012 than in earlier years when Eelgrass persisted throughout the bay, the 2012 temperatures rarely exceeded 20 °C and did not approach the thresholds shown to cause Eelgrass loss in northern waters (Fig. 4).

Taken in concert, the accumulation of clipped and shredded shoots indicative of Green Crab damage along the shoreline of upper Casco Bay, the growth and survival of Eelgrass during this experiment when Green Crabs were excluded, the observed destruction of Eelgrass in my experimental plots in a manner consistent with Green Crab damage, and negative evidence regarding other major potential threats to Eelgrass in Casco Bay implicate Green Crab bioturbation as a leading cause of Eelgrass loss from this system. Disney et al. (2014) also reported loss of an Eelgrass bed in Frenchman Bay, off Mt. Desert Island, ME, between 2012 and 2013 that coincided with the coast-wide increase in Green Crab populations.

Although acute effects of other potential stresses on Eelgrass in Casco Bay, such as toxic compounds (Short and Wyllie-Echeverria 1996) or unknown pathogens, seem unlikely, they cannot be ruled out, nor can potential interactive effects of various environmental stressors. For example, although the median light availability to the Eelgrass transplants measured during this experiment (19–23% of surface irradiance at mid-tide) exceeded the minimum light requirements reported for Eelgrass (10–20% of surface irradiance; Duarte 1991, Moore et al. 1997, Olesen and Sand-Jensen 1993), local observations suggested that turbidity in Maquoit Bay increased following the loss of Eelgrass, presumably due to resuspension of the fine bottom sediments (D.R. Devereaux, Brunswick Department of Marine Resources and Harbor Management, Brunswick, ME, and P.J. Horne, Freeport, ME, pers. comm.). The magnitude of underwater light attenuation during the Eelgrass decline is unknown, but it is possible that Green Crab bioturbation may have increased the concentration of suspended sediments in the system and accelerated the loss of Eelgrass through decreased light availability. In a Gulf of St. Lawrence estuary in Nova Scotia, Garbary et al. (2014) observed that in addition to increasing local turbidity, sediment resuspended by Green Crab foraging activity was also deposited heavily on Eelgrass leaves, where it contributed to further light reduction. In addition, warmer water temperatures are known to exacerbate the effects of light reduction on Eelgrass (Bintz et al. 2003, Moore et al. 2014, Neckles et al. 1993, Olesen and Sand-Jensen 1993). Thus, although the 2012 water temperatures did

not appear high enough to be the primary cause of Eelgrass loss, water temperature may have influenced Eelgrass response to presumed turbidity increases. There is a relative paucity of information on the simultaneous influences of multiple stressors on seagrasses (Orth et al. 2006a), and whether various factors may have enhanced the effects of Green Crabs or combined to cause Eelgrass loss is unknown.

The conclusion that Green Crabs were a primary cause of Eelgrass disappearance from Casco Bay is consistent with their documented role in causing dramatic declines of Eelgrass from some bays on Nova Scotia's Gulf of St. Lawrence (Garbary et al. 2014) and Atlantic (MTRI and Parks Canada 2014) coasts in the early to mid-2000s. There are distinct differences, however, between the Eelgrass–Green Crab relationships observed in Nova Scotia and Casco Bay. Genetic evidence indicates that Green Crab populations in the northwest Atlantic were established through multiple invasions from Europe (Blakeslee et al. 2010, Roman 2006). The Green Crabs first introduced to New York and southern New England in the early 1800s most likely originated from western Europe (Darling et al. 2008, Roman 2006). Populations expanded northward up the coast of New England and around the Bay of Fundy, reaching Nova Scotia's Atlantic coast by the mid-1950s. In the late 1980s or early 1990s, new genetic lineages were introduced to northern Nova Scotia that most likely originated from northern Europe (Darling et al. 2008, Roman 2006). These new genotypes expanded rapidly north and west into the southern Gulf of St. Lawrence and south along Nova Scotia's Atlantic coast into the Gulf of Maine (Pringle et al. 2011). The Green Crab destruction of Eelgrass that occurred in Nova Scotia estuaries was caused by the new invasion from northern Europe into areas either where Green Crabs did not yet exist (Gulf of St. Lawrence, Garbary et al. 2014) or where only Green Crabs of the historical (western European) lineage had existed previously (Little Port Joli and St. Catherine's Estuaries on the Atlantic coast, McCarthy 2013). Based on intra- and interspecific competition experiments in the Canadian Maritime Provinces, Rossong et al. (2012) suggested that the foraging ability of the recent northern-European lineages of Green Crabs may be superior to that of the long-established historical lineage, and that both time since establishment and genetic traits may influence the effects of Green Crabs on native habitats. Although the northern Green Crab genotypes are expected to continue expanding southward in the Gulf of Maine with the Gulf of Maine Coastal Current (Pringle et al. 2011), their southern limit in 2013 was Mt. Desert Island, ME; the northern lineages had not yet appeared in Casco Bay (Williams et al. 2015). Thus the destruction of Eelgrass habitat in Casco Bay was associated with a population explosion of the historical Green Crab genetic lineage. Davis and Short (1997) observed Green Crab bioturbation of transplanted Eelgrass in New Hampshire, but the loss of Eelgrass in Casco Bay represents the first documentation of damage to natural beds by the historical Green Crab lineage. Green Crab disturbance of Eelgrass in its native Europe, where Green Crab populations appear to be regulated by parasites (Torchin et al. 2001), has not been reported, nor am I aware of impacts to Eelgrass along other coasts where Green Crab invasions overlap Eelgrass distribution (west coast of North America, Japan).

Although a tremendous variety of Green Crab prey items have been identified, bivalve mollusks often dominate their diet (Cohen et al. 1995, Glude 1955, Grosholz and Ruiz 1995, 1996, Klassen and Locke 2007, Ropes 1968). Indeed, the recent Green Crab population explosion in coastal Maine has been deemed a severe threat to the state's present-day Soft-shell Clam industry (MDMR 2013, Webber 2013). The range of sediment disturbance caused by Green Crab foraging varies from the top few centimeters to pits 10 cm–15 cm deep (Cohen et al. 1995, Garbary et al. 2014), and Green Crab impacts on prey are greatest in soft-bottom habitats (Klassen and Locke 2007). Both the fine-grained sediments in upper Casco Bay (Kelley et al. 1987) and the broad distribution of Soft-shell Clams as a preferred prey item (MDMR 2009) may have concentrated Green Crab digging activity in this area. Garbary et al. (2014) observed that as sediments become loosened by Green Crab foraging, Eelgrass shoots become easily dislodged; thus, the fine sediments in upper Casco Bay may have further increased Eelgrass susceptibility to Green Crab disturbance. By the time of my exclosure experiment in 2013, Green Crab predation had depleted much of the bivalve food resource in Maquoit Bay (pers. observ.), but *Nassarius obsoletus* (Say) (Mud Snail; formerly *Ilyanassa obsoleta* [Say]; ITIS 2015) was extremely abundant; Mud Snails are common prey of Green Crabs (Schwab and Allen 2014) and the high Mud Snail density could explain the continued crab activity in Maquoit Bay. Green Crabs are known to disturb Eelgrass transplants during restoration projects (Davis and Short 1997), and the disturbance to the unprotected Eelgrass shoots outside my exclosures could have been caused by Green Crabs foraging for benthic prey or by the direct grazing by juvenile Green Crabs on Eelgrass meristems (Malyshev and Quijón 2011).

Implications for Eelgrass recovery

Recovery of the Eelgrass meadows in upper Casco Bay will depend on processes controlling Eelgrass recruitment, survival, and growth. Natural Eelgrass revegetation following large-scale declines occurs through germination and survival of seedlings to form new patches and subsequent lateral expansion of patches by vegetative propagation (Greve et al. 2005, Harwell and Orth 2002a, Olesen and Sand-Jensen 1994). In the early 2000s in Maquoit Bay, the mean rate of new-patch recruitment into a 32-ha scar in the existing Eelgrass meadow that had been denuded by commercial dragging for *Mytilus edulis* L. (Blue Mussel) was 0.19 patches m^{-2} yr^{-1}, a rate comparable to published values from other systems (Neckles et al. 2005). At that time, the denuded drag scar was surrounded by dense Eelgrass beds to provide a ready and abundant supply of seeds for recolonization, and aerial photography 10 years post-dragging showed that Eelgrass in the former scar had not yet reached 100% cover (J.W. Sowles, North Yarmouth, ME, unpubl. data). In contrast, following the recent extensive loss of vegetation from most of upper Casco Bay, the closest dense stand of Eelgrass to the midpoint of Maquoit Bay is 15 km away (northeastern limit of 2013 Eelgrass distribution; Fig. 1). Eelgrass seeds can be transported long distances by floating reproductive shoots (Harwell and Orth 2002b), so the Eelgrass beds in lower Casco Bay should serve as a source of seeds

for recolonizing upper Casco Bay. However, the rate of new-patch recruitment from such distant seed sources would presumably be considerably lower than the rate measured from adjacent beds, thus resulting in a slower recovery.

Eelgrass revegetation would likely be hastened substantially by restoration (e.g., Orth et al. 2006b, Short et al. 2002). Recently, effective control of Green Crabs through trapping has allowed successful Eelgrass restoration in Little Port Joli Estuary on the Atlantic coast of Nova Scotia (MTRI and Parks Canada 2014), although the Green Crab population threshold for vegetation survival is as yet unknown (Kanary et al. 2014). Management interventions to control Green Crabs are similarly being considered in Maine (MDMR 2013). Historical evidence suggests that the abundance of Green Crabs in New England is regulated at least in part by water temperature, with population declines following periods of colder than average temperatures (Berrill 1982, Welch 1968). Although it is unknown whether Green Crab populations in coastal Maine will decline naturally or will require management control, results of my exclosure experiment suggest that natural recovery or restoration of Eelgrass in upper Casco Bay may be impossible until Green Crab population levels have decreased.

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